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RESEARCH ARTICLE - ANTS

A New Protocol Using Artificial Seeds to Evaluate Dietary Preferences of Harvester Ants in Semi-arid Environments

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Abstract

The preferences of seed intake by harvester ants (*Pogonomyrmex* spp.) have been debated for a long time, mainly due to the lack of repeatable methods to draw clear conclusions. However, several characteristics of the food resource are well recognized as the drivers of such selective predation. For instance, resource quality (i.e., availability of carbohydrates, lipids, and proteins) is one factor that could explain the observed foraging patterns of *Pogonomyrmex* species. In this sense, experimental approaches using artificial resources (e.g., synthetic seeds/diaspores) have provided a useful and alternative tool to study ant's food foraging behavior. Therefore, it is expected that the use of artificial seeds also could offer a versatile way to assess the influence of resource quality on the resource selection by harvester ants. On the other hand, empirical experiments involving harvester ants and artificial seeds are still rare in the literature and it is not known if such methodology is efficient with different *Pogonomyrmex* species. In this study carried out in a Neotropical arid environment of central Mexico, we tested a simple but fundamental question: Do harvester ants (*Pogonomyrmex barbatus*) predate artificial seeds with manipulated nutrient content (lipids and proteins) in the field? We found that the proportion of native seeds removed was lower than the proportion of artificial seeds removed. However, we found no difference between the removal of artificial seeds containing only lipids and the seeds containing lipids + proteins. These findings indicate that the artificial seeds synthesized by us could be an effective method to test different ecological hypothesis involving harvester ants. Moreover, our empirical experiment offers a benchmark to study the influence of resource quality on the food foraging behavior of harvester ants in Neotropical arid environments.

Introduction

Seed predation is widespread among ants, mainly in arid environments where harvester ants are ecologically dominant (Wilson & Hölldobler 1990; Taber 1998; Rico-Gray & Oliveira 2007; Dáttilo & Rico-Gray 2018). In the American continent, harvester ants (*Pogonomyrmex* spp. Mayr, 1868) are recognized as one of the main seed predators, since they influence the ecological dynamics of natural communities by exerting effects on the spatial distribution and demography of plants (MacMahon et al. 2000; M. Herrera & Pellmyr 2002). However, although the ecology of *Pogonomyrmex* species is well studied in northern and southern environments of the New World (MacMahon et al. 2000; Pirk & De Casenave 2006; Pirk & De Casenave 2011), little is known about the ecology of harvester ants in Neotropical arid environments (but see García-Chávez et al. 2010; Belchior et al. 2012; Guzmán-Mendoza et al. 2012).

As central place foragers, the foraging activity of *Pogonomyrmex* species is limited to small distances (between 5 to 25 m) around their nests (Holder & Polis 1987; MacMahon et al., 2000; Pirk et al., 2009; Belchior et al., 2012). To avoid the costs generated by having such limited foraging areas, *Pogonomyrmex* harvester ants predate seeds from a great variety of plant species (Rico-Gray & Oliveira 2007), and in some cases, a unique ant colony can predate seeds up to 30 different plant species (Pirk et al., 2009; Belchior et al., 2012). However, most of *Pogonomyrmex* species exhibit particular

preferences in their seed intake, predating some plant species more than others (i.e., differential seed predation) (Taber, 1998; MacMahon et al., 2000; Rico-Gray & Oliveira, 2007). On the other hand, in the wide geographical distribution of *Pogonomyrmex* species, there is not a consensus about their seed preferences and which are the main factors influencing the seed selection by harvester ants (MacMahon et al., 2000; Pirk & De Casenave, 2006; Belchior et al., 2012; Schmasow & Robertson, 2016). In addition, in arid environments, where harvester ants are found, the landscape is highly heterogeneous (in terms of vegetation, climatic conditions, topography and geology) in both spatial and temporal scales (Bestelmeyert & Wiens 2001; Rietkerk et al., 2002; Whitford, 2002), which has led to the implementation of particular methodologies conceived to be used in a given arid environment (since they cannot operate in the same way and need to be readjusted for other localities (e.g. Huenneke et al., 2001)

Although there is no agreement about which factors shape the differential predation of seeds, studies have showed that some factors can directly influence the seed selection by *Pogonomyrmex* spp., such as: spatial abundance and richness of plants (MacMahon et al., 2000; Pirk & Lopez De Casenave, 2006), nutritional quality of seeds (Whitford & Steinberger, 2009; Schmasow & Robertson, 2016), seed size (MacMahon et al., 2000; Pirk & de Casenave, 2010; Pirk & de Casenave, 2011), seed density (Flanagan et al., 2012), and the seed distance from the nests (Hölldobler, 1976; Holder & Polis, 1987; Schmasow & Robertson, 2016). However, due to the difficulty to test ecological hypothesis in the field that consider the effect of seed traits (e.g., nutrient content, morphology and physiochemical defenses) on the differential predation by *Pogonomyrmex* species, these questions have been rarely explored.

On the other hand, the use of artificial methods in experimental protocols has proved to be an excellent benchmark to test ecological hypothesis in the field, mainly because they can be implemented and repeated in different environments and under different conditions (e.g. Dáttilo et al., 2016; Roslin et al., 2017). In this sense, some studies have implemented the use of artificial seeds to evaluate dietary preferences by ants (Raimundo et al., 2004; Bieber et al., 2014; Rabello et al., 2014). Specifically for harvester ants, Whitford and Steinberger (2009) used artificial seeds with manipulated nutrient content and found that the harvester ant *Pogonomyrmex occidentalis* (Cresson, 1865) exhibits preferences for seeds with different protein content in North America. In fact, the use of artificial seeds could be an alternative tool to study the seed intake by *Pogonomyrmex* harvester ants, since this subject is supported by little empirical evidence in the literature. However, it is not known if the approach of artificial seeds is efficient for all the *Pogonomyrmex* species, particularly in the Neotropical region. Therefore, in this study we synthesized two types of artificial seeds containing different proportions of lipids and proteins to test if one harvester ant distributed in Neotropical regions [*Pogonomyrmex barbatus* (Smith, 1858)] could discriminate among native and artificial seeds with manipulated contents of lipids and proteins in a Mexican semi-arid environment.

Methods

Study area

The study was conducted during April 2017 within the Neotropical semi-arid region of Zapotitlán, state of Puebla, Mexico, located within the Biosfere Reserve of Tehuacán-Cuicatlán. The mean altitude is 1,400 ma.sl., annual mean precipitation is 400mm and the mean temperature is 22° C (Zavala-Hurtado et al., 1996 and references therein). The vegetation of this region can be categorized as a xeric shrub land (Rzedowski, 2006), and the plant association where we performed the study corresponds to "tetechera", in which the dominant plant species are the columnar cactus *Neobuxbaumia tetetzo* (J.M. Coult.) Backeb. (Cactaceae), and the thorny shrubs *Prosopis laevigata* (Willd.) M. Johnston (Fabaceae), *Mimosa luisana* Brandegee (Fabaceae), *Parkinsonia praecox* (Ruiz &Pav. ex Hook.) Hawkins (Fabaceae) and *Vachellia constricta* (Benth.) Seigler and Ebinger (Fabaceae) (Zavala-Hurtado, 1982, Pavón et al., 2000, Dáttilo et al., 2015). The study area exhibits strong seasonality, with a long dry season from October to May and a short rainy season from June to September.

Artificial seeds

We synthesized two types of seed, one with lipids (9% of the content) and other with lipids and proteins (9% and 6% of the content respectively). Artificial seeds were prepared by mixing 150 g of wheat flour, the desired amount of casein protein, 100 ml of water and 25 ml of vegetable oil. The addition to the vegetable oil served to mask the small differences in caloric value of the wheat flour and casein (see Whitford & Steinberger, 2009). We used these nutrients since ants can forage selectively for protein, lipids and carbohydrates to redress specific colony requirements (e.g. ontogeny) (Mayntz et al., 2005; Whitford & Jackson, 2007; Dussutour & Simpson, 2008). Moreover, it is worth to mention that the content of our mixture represents highly nutritive resources, thus, they can influence the foraging behavior of harvester ants (Crist & MacMahon, 1992; Whitford & Steinberger, 2009; Schmasow & Robertson, 2016). The mixture was poured in a thin layer and allowed to air dry for 24h before the experiments. We then cut the dried mixture into smaller pieces of the same size (4 × 4 mm) (Fig 1).

Sampling design

In order to test if *P. barbatus* predates artificial resources containing lipids or both lipids and protein, we selected 14 active colonies of the harvester ant *Pogonomyrmex barbatus* (Smith, 1858) (Myrmicinae). In order to control the effect of colony size (i.e. number of ants), we used only colonies that presented mounds of approximately one meter in diameter.

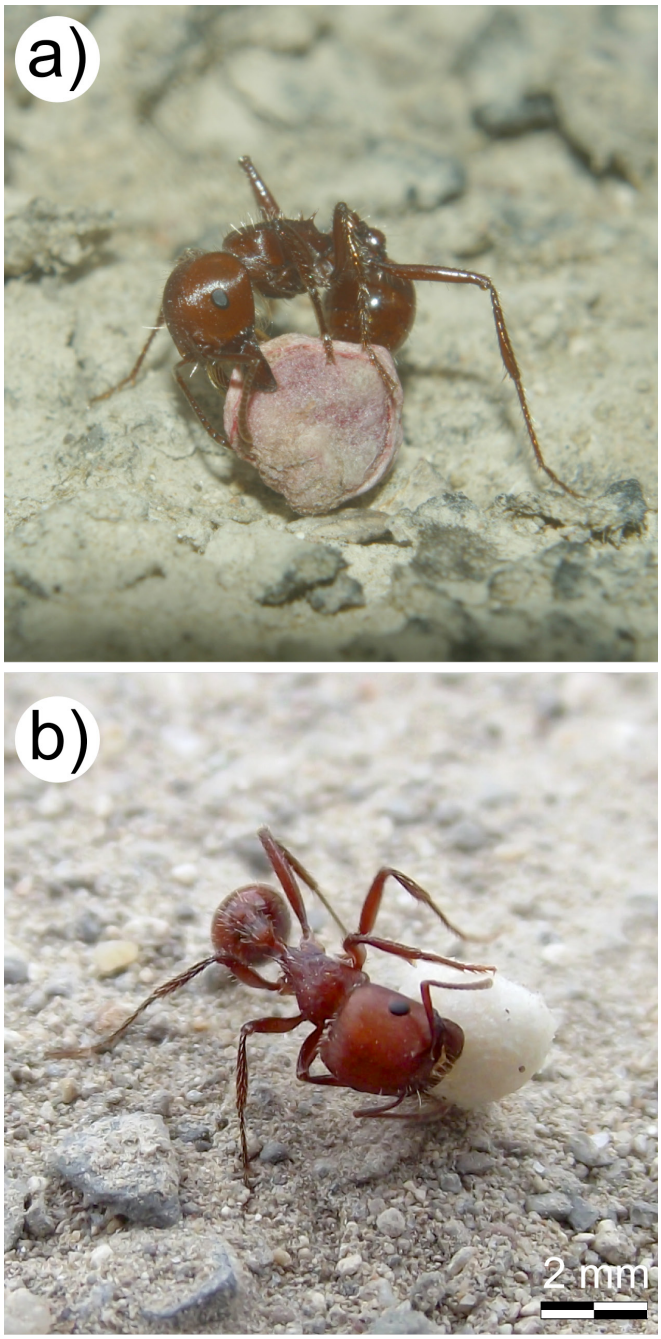

Fig 1. Workers of *Pogonomyrmex barbatus* (Myrmicinae) manipulating seeds: (a) of *Opuntia pilifera* (Cactaceae) and (b) artificial seeds with lipids (9% of the content). Photo credits: (a) J. H. García-Chavez and (b) P. Luna.

We used three types of seeds: a non-artificial native seed from *Opuntia pilifera* F.A.C. Weber (Cactaceae) (mean size ± SE: length = 3.85 ± 0.07 mm, width = 3.78 ± 0.09 mm, n=20), and the two artificial seeds synthesized by us, with lipids (9% of the content) and with lipids and proteins (9% and 6% of the content, respectively). We selected *O. pilifera* since it is frequently used by the ants and are widely distributed in the study area (Luna 2016; Luna et al., 2018). Moreover, it is well documented the predation of *Opuntia* spp. Mill. seeds by harvester ants (González-Espinosa & Quintana-Ascencio, 1986; Montiel & Montaña, 2003; Gárcia-Chavez et al., 2010).

In order to establish the experimental units, first, we selected a random orientation in respect to the entrance of the *P. barbatus* colonies. Then at a distance of four meters, in the selected orientation, we eliminated all branches and small rocks and leaves on the soil surface, leaving three 20 x 20 cm quadrants of bare soil with a distance of 10 cm between them. Approximately 24 hours later, we placed 20 seeds of each category (i.e., native, only lipids or lipids + proteins, respectively) within each quadrant. The seeds were placed at 06:00h (before starting the activity of the ant colonies) and were checked 12 hours later to count the number of seeds removed. We visited the colonies 24 hours after the experiments to verify if the ants left the seeds out of the colony, which did not happen with any seed type in any colony. We took care that only ants removed the seeds. In fact, in a previous study in the region, García-Chavez and collaborators (2010) showed that ants are the dominant seed predators, displacing birds and rodents.

Data analysis

Since our experimental design corresponds to a mixed effect model, we applied a generalized linear mixed model with a binomial error distribution with *logit* link (Crawley 2012) to test if the proportion of seeds removed at the end of the experiment differs between the seed types (native, lipids and lipids + proteins). For our data analysis, the fixed effect was seed type (native, lipids, and lipids + proteins) while the random factor was the ant colonies. In addition, we applied a *post-hoc* analysis to look for differences between the levels of the factor "seed type" through Wald χ^2 tests. All analysis where performed in R (version 3.4.0) (R Core Team 2017) with the packages *lme4* (Bates et al. 2015) and *phia* (Helios 2015).

Results

We found that all of the studied colonies removed the offered artificial seeds. Further, we observed that the proportion of removed artificial seeds containing only lipids reached 100% in five colonies (35.7%), while the proportion of seeds removed containing lipids and proteins reached 100% in seven colonies (50%). Moreover, we recorded no removal of native seeds in seven colonies (50%). Note that, we observed ants from the genus *Pheidole* Westwood, 1839 (Myrmicinae) in contact with the artificial seeds in two experimental units, but we did not record any removal by this ant genus.

We observed that, the seed type predicted the proportion of seeds removed ($\chi^2 = 120.31$, df = 2, $P < 0.001$). Specifically, the proportion of native seeds removed was lower than the proportion of artificial seeds removed (*post-hoc:* native *v.s.* lipids: $\chi^2 = 103.63$, $df = 1$, $P < 0.001$; native *v.s.* lipids + proteins: $\chi^2 = 115.51$, $df = 1$, $P < 0.001$) (Fig 2). However, we found no difference in the number of seeds removed between the artificial seeds containing only lipids and both lipids and proteins (*post-hoc* lipids *v.s.* lipids + proteins: $\chi^2 = 1.968$, df = 1, $p = 0.16$) (Fig 2).

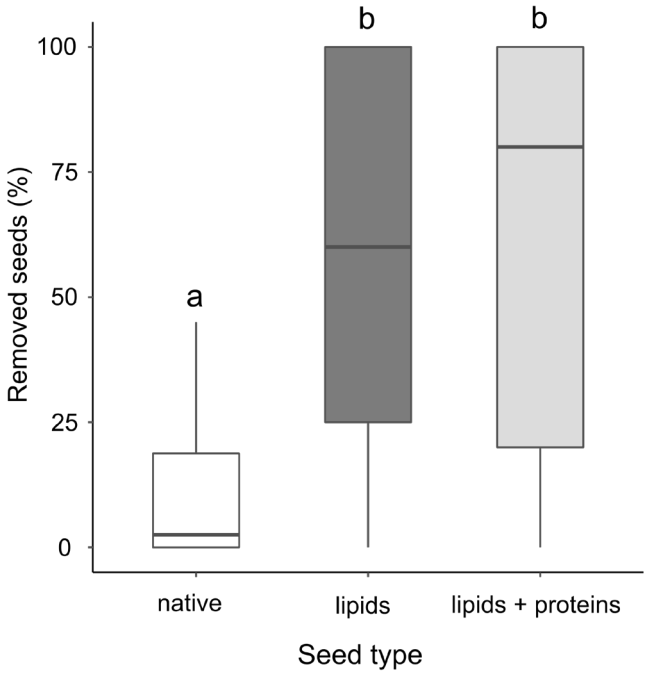

Fig 2. Proportion of removedseeds by *Pogonomyrmex barbatus* (Myrmicinae). Native seed = *Opuntiapilifera* (Cactaceae). Lipids = artificial seeds with lipids (9% of the content). Lipids + proteins= artificial seeds with lipids + proteins (9% and 6% of the content, respectively). The lines represent the first and four quartiles, the box represents the second and first quartiles and the line within the box represents the median of each treatment. Boxplots with different letters represent significant differencesaccording toWald χ^2 tests.

Discussion

We found that the proportion of native seeds removed is lower than the proportion of artificial seeds removed. However, we found no difference between the removal of artificial seeds containing only lipids (9% of the content) and the seeds containing lipids + proteins (9% and 6% of the content, respectively). These findings confirm that harvester ants can predate artificial resources containing lipids and proteins despite its non-native "identity" as previously reported for other ant species (Mayntz et al., 2005; Whitford & Jackson 2007; Dussutour & Simpson, 2008). Further, our results show that the use of artificial seeds could be a good option to study the influences of resource quality in the diet of harvester ants, since *P. barbatus* removed more artificial seeds than the native seeds using a standardized experiment in the field. In addition, the artificial seeds not only attracted *P. barbatus*, since we recorded *Pheidole* ants in contact with our artificial seeds. Therefore,it is expected that our artificial seeds could also attract other granivorous (seed eaters) and omnivores (those that scavenge and feed on plant exudates) ants (Mayntz et al., 2005; Dussutour & Simpson, 2008).

The season in which we performed the experiments correspond to the dry season, just when *P. barbatus* present a narrower niche breath and smaller home ranges compared to the rainy season (Guzmán-Mendoza et al., 2012). Despite the foraging strategies of *P. barbatus* in the dry and warm season, we found that *P. barbatus* can switch its foraging activity into the harvest of novel resources (artificial seeds in this case), leaving behind a commonly predated resource (seeds of *O. pilifera*) (García-Chávez et al., 2010). Additionally, the complete removal of artificial seeds in many ant colonies, suggest that workers of *P. barbatus* can rapidly focus its foraging efforts on the collection of highly nutritious resources. The higher predation rates on resources with manipulated contents of lipids and proteins suggest that the food quality is quickly communicated among foragers, leading to a greater number of recruited workers to the seed patch (Whitford & Steinberger, 2009; Flanagan et al., 2012). Moreover, the non-rejection of our artificial seeds shows that our they could be stored for further consumption (MacMahon et al., 2000).

In conclusion, we found that our manipulation of lipids and proteins in the artificial seeds generated an increase in the seed predation rates by *P. barbatus*, which indicates that the manipulation of nutritional components could be useful on future experiments. Therefore, the experiment conducted by us using artificial seeds offers an excellent benchmark to study the influence of resource quality on the food foraging behavior of harvester ants in Neotropical arid environments. However, note that the results of our experiments could be restricted to the red harvester ant *P. barbatus* since we do not know how other *Pogonomyrmex* species could react to our artificial seeds. Morevoer, it is important to mention that to draw clear conclusions about the differential seed predation by harvester ants, and to answer particular ecological hypothesis, the use of artificial seeds require an adequate experimental design. In short, our study is, therefore, an important advance to implement repeatable methods in the study of harvester ants in order to better understand its influence as seed predators on ecological communities.

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